

**CALOPRYMNUS CAMPESTRIS.  
ITS RECURRENCE AND CHARACTERS.**

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[Read October 13, 1932.]

PLATES VII. TO IX.

INTRODUCTION.

In September, 1931, the writer received<sup>(1)</sup> from Mr. L. Reese, of Appamunna, in the far north-east of South Australia, a skin and skull of *Caloprymnus campestris*, the first to be taken since the three original specimens on which Gould founded his description of the species in 1843. After 90 years the reappearance of this mammal, unrepresented in any Australian collection and long since thought to be extinct, was as gratifying as it was unexpected, and called for prompt action in adding by personal observation in the field as much as possible to the very imperfect accounts of its natural history which have so far been given. Accordingly, in December, the writer proceeded to the scene of the first occurrence, and in four weeks' work there met with considerable success both in obtaining further specimens and in collecting data on the general economy of the animal.

This success was very largely due to the cordial co-operation of Mr. Reese, whose services are hereby gratefully acknowledged.

DISTRIBUTION.

The locality from which the first specimen was taken in August, 1931, was near Cooncherie water hole, about 18 miles south of Clifton Hills Station on the lower Diamantina in South Australia, in lat., approximately, 26° 32' south. As a result of investigation following the first record its proved distribution may be extended over a large area of the eastern portion of the Lake Eyre Basin, specimens and reliable records from observers personally known to the author having been obtained from as far south as Lake Harry and as far north as Coorabulka in South-West Queensland. The north and south limits of its range, as at present ascertained, are, therefore, approximately, lats. 23° 40' and 29° 21' south. No records have so far been obtained west of Lake Eyre and the Kallakoopah, and the furthest easterly occurrence is at Innamincka, on the Barcoo, in long. 140° 49' east. The area thus defined is referred to in the sequel as the "proved" area and is indicated on the map<sup>(2)</sup> (fig. 1).

The exact locality from which Sir George Grey's original specimens came is, unfortunately, not known, Gould, in 1843, simply stating (quoting Grey?) that "it inhabits the stony and sandy plains of the interior of South Australia." If the assumption is made that the specimens were taken at least a year prior to the publication of Gould's description in London, in 1843, it might appear that they came from a district considerably south of the lowest point of the "proved" area on the map, since at that time no official parties had penetrated it. The most northerly and north-easterly points reached by Eyre in his third expedition, in 1840 (Eyre's

<sup>(1)</sup> See Trans. Roy. Soc. S. Austr. (1931), vol. lv., p. 162.

<sup>(2)</sup> For assistance in compiling this map I am indebted to Mr. C. T. Madigan, of the University of Adelaide, and to Mr. E. J. Kenny and Mr. L. C. Ball, of the Geological Surveys of N.S.W. and Qld., respectively.

lookout and Mount Hopeless), lie on its southern fringe, but in the appendix on the fauna in his "Expeditions into Central Australia" no mention is made of the animal, as would surely have been the case had he obtained the three specimens

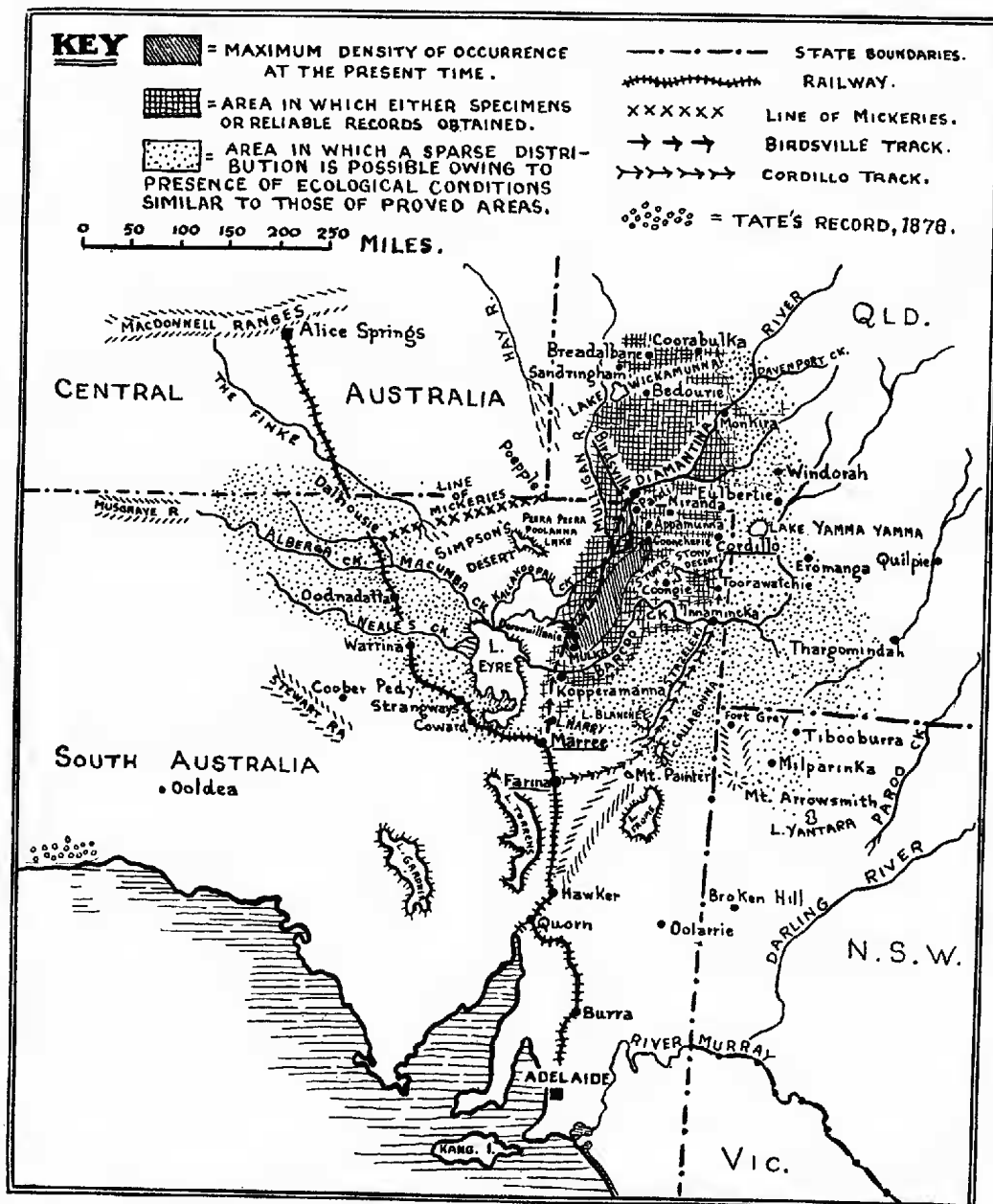


Fig. 1.  
Map, showing distribution of *Caloprymnus campestris*.

which ultimately found their way into the British Museum. Though the place of origin of these specimens is a matter of considerable interest, it has now become too speculative to be followed further here.

The distinctive physical features of the area in which its presence is now proved are produced by combinations of north and south sandridges, claypans,

and gibber plains. To the north and south of the proved area the extension of this environment is not great, but elsewhere, both east and west, similar combinations occur without fundamental alteration<sup>(3)</sup> of ecological conditions, and it is possible that careful field work, particularly on the gibber plains which stretch north and west from Lake Eyre to the Central Australian border, might result in a great extension of its known range. The difficulties of testing this by personal observation are, however, very great owing to the huge areas involved and the waterless nature of much of the country, and enquiry is hampered by the sparse occurrence of the animal itself and the disappearance of the native blacks. All evidence obtained from whites in this indirect way, moreover, must be accepted with great caution, as on the fringes of the area recently examined (though not within the area itself) species of *Bettongia* and *Lagorchestes* occur which are so similar to *Caloprymnus* that in popular estimation they call for no discrimination from it.

The single record of *Caloprymnus* in the literature, since the taking of the original specimens, is that of Tate [Trans. Phil. Soc. S. Austr., viii., p. 124 (1878)], who claimed it as a common form on the Bunda Plateau at the head of Great Australian Bight. The locality is 400 miles from the site of the present occurrence and presents very different features. Tate, apparently, took no specimens of the animal and produced no evidence in support of his identification, and such details of its habits as he gives are more applicable to *Bettongia lesueuri* or *B. penicillata*, both of which probably occurred in the area at that time. Although the possibility of the occurrence of *Caloprymnus* on the Nullarbor Plain and adjacent tracts is not to be altogether discounted, it would seem very probable that Tate was mistaken. Recent enquiry amongst the blacks by Mrs. Daisy Bates, of Ooldea, and Mr. A. G. Bolam, of Kingoonya, have produced no definite results. The blacks profess to recognise photographs of *Caloprymnus*, but as different individuals apply different names to it, and as the same individuals use different names at different times, their testimony is of little value. One point of interest, however, has been established by Mrs. Bates in these enquiries, namely that the word "Weelba," which Tate quoted as the aboriginal name for his "*Caloprymnus*," is of legendary significance only and denotes a mythical Rat Kangaroo whose burrowing activities, long ago in the "Dream Times," created the sandhills as a by-product. The name is not applied to any living species.

In the "proved" area several names are current amongst the remnants of the former tribes. The Yalliyandas call the animal Oolacunta; the Yaurorkas, Coorgee; and the Dicries, Wirtirec. In recent years the Wonkonguroos, an off-shoot of the Aruntas of the centre, have drifted south-west on to the Lower Diamantina and have largely replaced the Yalliyandas. It is of interest that they have adopted the Yalliyanda name Oolacunta for the animal, and some accomplished hunters amongst them state emphatically that in the country which they have left (the southern portion of Simpson's Desert) *Caloprymnus* does not occur.<sup>(4)</sup>

In ordinary years the Lake Eyre Basin is a most unattractive area from the point of view of the mammal collector, and the disappearance of *Caloprymnus* from scientific ken must be attributed rather to lack of systematic collecting than to any sudden change in the status of the animal in the fauna, following Grey's discovery. All the evidence obtained by questioning blacks goes to show that in

<sup>(3)</sup> The flood plains of the Diamantina and the Coongie lakes of the Barcoo give a somewhat Eastern fascies to parts of the tract in question, but the area involved in these inundations is so small a part of the total inhabited by *Caloprymnus* as to prevent one laying much stress upon them as factors influencing distribution.

<sup>(4)</sup> This is the more probable, as the absence of gibber plains from this area has recently been proved by Madigan's aerial reconnaissance. See Proc. Roy. Geog. Soc. S. Austr. Branch, 1928-29.

all probability it has had an uninterrupted tenure of the country, but it is equally certain that in normal times its numbers are small, since men like Mr. Reese, whose opportunities for observation are practically continuous throughout the year, affirm that in thirty-five years they have seen no more than twenty specimens.<sup>(5)</sup>

It is significant, too, in this connection that in the whole of the very considerable literature on the exploration of the Lake Eyre Basin, there is no unequivocal reference to the animal.

At the time of my passage through the area, conditions as they bear upon animal life were very favourable and quite supernormal as compared with average conditions over a series of years. A period of seven years of drought had been broken, and vegetation had been restored on a comparatively lavish scale. All species of mammals were undergoing a quick increase in numbers, and rodents especially had assumed plague proportions. Most of the specimens of *Caloprymnus* were obtained, and the bulk of the observations upon it were made, on two flats lying east and west of Cooncherie Sandhill. In general features they represent a transition belt between the true gibber plains and the loamy flats. Though stony, they present no expanse of pavements such as characterise the former, and vegetation is not reduced to vanishing point as it is there. There is a fair sprinkling of plants, particularly of species of *Kochia*, *Atriplex*, *Bassia*, and *Eremophila*, though always widely spaced and never forming communities sufficiently dense to afford much shelter even to the smallest mammals. Here and there, at long intervals, occur little clumps of the so-called cork wood (*Hakea Ivoryi*), here a stunted tree of 10 or 15 feet.

The numbers occurring in this particular locality were very considerable. In the course of a week's riding on the two flats over an area of perhaps 20 square miles, 17 *Oolacuntas* were sighted. This, however, is no index to the density of its occurrence elsewhere, as in some other tracks presenting very similar features few or none were seen. It is possible that the increase in its numbers which has taken place since the drought is yet in its early stages, and that if conditions remain favourable its distribution may become more even and more dense. All the evidence obtained so far goes to show that its distribution at present is highly discontinuous but that it follows in a general way the fringes of the gibber plains, where conditions are as described. Although tracks were occasionally seen crossing the sandhills, it appears to spend little time in them and does not nest there.

#### HABITS.

Although its mode of occurrence in isolated areas might be thought favourable to the development of a gregarious habit, this is by no means so. On the contrary the animal appears to be exceptionally solitary, since all those seen, both males and females, were put up singly, and on no occasion was a female accompanied by an independent young one. It is remarkable that *Caloprymnus* is the only terrestrial mammal<sup>(6)</sup> of the area which has not adopted a fossorial habit. It retains the primitive nesting habit of the *Potoröinae* in spite of its apparent inadequacy in a shelterless region of intense heat and intense illumination. The nest,

<sup>(5)</sup> Regret may here be expressed that the splendid work of Professor Wood-Jones on South Australian mammals, involving probably the most prolonged and extensive enquiry ever undertaken in this field in Australia, was not rewarded by the re-discovery of the animal. In 1924 he was within an ace of so doing, as Mr. L. Reese in that year gave him some account of the animal which I have now shown to be *Caloprymnus*; but as no specimens were forthcoming and he was not free to undertake the field work necessary for its identification, the matter lapsed.

<sup>(6)</sup> With the exception of *M. rufus*, which however spends the heat of the day camped in the shade of the timber near the channels, and possibly of *Choeropus*, about which little information is as yet available.

however, is a modified one built into a shallow excavation, frequently under a cotton or saltbush, but quite often in a most exposed situation well away from any shrubs of size. The excavation takes the form of a circular pan, 10" in diameter and 4" deep, with almost vertical walls cut away on one side to form a shallow entry and exit passage. The cavity is lined with leaves and grasses, and when it is situated in the open it is thatched by laying twigs and grass stems across the top and fixing them in position by interlacing them with stumps of plants formerly growing round the hole. The site appears always to be chosen with a view to a sufficiency of small growth round the nest to provide the thatch, which is evidently not carried to it. The blacks say that if the animal is frequently disturbed it deserts the nest and builds again elsewhere; many of the nests examined by me showed well-defined pads radiating out in several directions and apparently indicating a tenancy of some duration. Nevertheless, the whole structure has an air of impermanence and crudity very different from that of some of the other Bettongs, and this impression is heightened by its extraordinary habit of protruding its head through a gap in the thatch for purposes of observation. This habit is consistently vouched for by the blacks, who capture the animal by first ascertaining the direction in which the opening faces, and then, if the wind is suitable, creeping up from the opposite side and laying their hands, or a coolamon, over the top. Two specimens were actually obtained in this way by a Yalliyanda man during my stay at Cooncherie.

Observation of the undisturbed and unsuspecting animal has not been possible, and such impressions of its appearance and mannerisms as have been gained have resulted from chance encounters and from watching the animal while galloping it down. Most of the specimens were got in this way, six horsemen participating. The procedure adopted was to ride over a chosen area of the plain in extended order till an *Oolacunta* was put up. The nearest rider then galloped it towards the sandhill, while the rest of the party remained in a group. Before reaching the sandhill the animal was headed off by the pursuer and returned on its tracks towards the party; when the first horse began to flag it was replaced at a suitable moment by a fresh one, and so on. The performance of the animals coursed in this way varied somewhat, young males giving a better account of themselves than females, but in every instance a turn of speed was developed quite surprising in so stockily built an animal. This, of course, was particularly noticeable at the beginning of each chase, and the end of the first lap was always a moment of considerable excitement, as the heading process called for the utmost from the horses, and if not turned at this point the *Oolacunta* gained the sandhills and usually escaped.

The gait at this speed is distinctive and appreciably different from that of the *Bettongia* species and of *Aepyprymnus*, though the differences do not lend themselves to easy definition. It moves at an easy, uniform stride, which was not modified in character at any stage of the chase; the trunk is carried leaning well forward, and the tail is almost straight. In connection with its gait a very remarkable characteristic becomes apparent on inspection of the tracks, namely, that when moving at speed the feet are brought down rather widely separated from side to side and *one in advance of the other*. Unfortunately, the tracks made by those animals actually observed on the move were too indistinct to be of value, the ground being stony and dry, but on the claypans, *Oolacunta* tracks made during the last wet, were common and were of two types. When the animal is moving on all fours, using the tail as a support, the track is the one normal in all macropods (fig. 2A). But when the manus and tail are no longer impressed and the animal resorts to saltation, the tracks take the form shown in fig. 2B, the right toe being brought down well in advance of the left, and with its long axis in the line of advance, whereas its fellow is rotated outwards through about 30°. Each pair of

imprints is identical, and there is no alternation of right foot with left in the advance. All tracks examined showed the features described with little modification, except in the length of the stride, and one particularly well-defined track crossing a claypan yielded the following measurements:—The antero-posterior interval separating the base of the right toe from the base of the left was 6"; the lateral separation, 1"; and the length of stride, from the apex of toes in two sets of imprints, 30".

These peculiarities of the tracks are, of course, well known to the blacks, and before any were seen by the writer one of the Wonkonguroo hunters, who was familiar with the Kanunka (*B. lesueuri*) in the Mickerie country, pointed out as a great marvel how two animals so alike as the Oolacunta and Kanunka should make tracks so different. He drew diagrams in the sand illustrating the differences; *B. lesueuri* making (as is well known) normal macropod tracks in which the toes are placed close together, nearly parallel, and with heels and toes opposite one another across the midline. Being aware of this asymmetry in the tracks before the living animal was seen, it was a matter of great interest during the subsequent encounters to correlate it by observation with the gait of the animal while on the move. No definite results were so obtained, however, as the thin pale legs fade out in a remarkable way against the yellow-grey background, and the

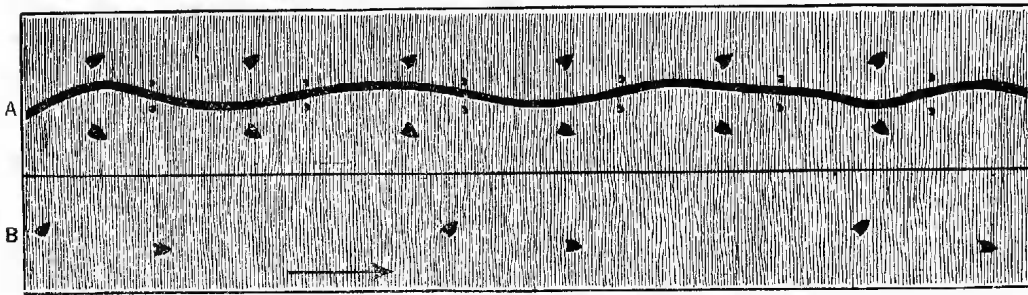


Fig. 2, A and B.  
Diagram of tracks of *Caloprymnus campestris*.

difficulties of close observation on so small an object, from a galloping horse, are also considerable.

None of the Oolacuntas coursed showed any inclination to dodge or double; they kept direction with great constancy till headed by the horse, and then turned without spectacular bounds, such as are recorded for *Lagorchestes*, sp. Far more remarkable than its speed is the endurance of the animal. The first specimen taken, a young male, ran twelve miles and wore down two horses before he was finally brought to a standstill with a third, and all this under such adverse conditions of excessive heat and rough going as to make it almost incredible that so small a frame should be capable of so immense an output of energy. Each of the seven examples secured by this method persisted to the very limit of their strength and, quite literally, they stopped only to die.

Later an adult female and large-furred pouch young were obtained undamaged from a nest, and these specimens were kept alive for a short time and furnished the only photographs of the living animal which were obtained. Their behaviour when handled was mild and gentle, and unlike the other Bettongs they made no attempt to bite, but voiced their protest with the only sound noted at any time in connection with the animal—a harsh aspirate sound, little characteristic and similar to that made by many other marsupials of both suborders. The animal

has no characteristic smell and the only ectoparasite noted was a sparsely occurring louse, not yet examined.

The stomach contents of all specimens obtained were examined, but without definite findings. At this time of the year the animal appears to be a night feeder, and as most of the specimens were got towards the middle of the day, little undigested material remained in the stomach. The accounts of its feeding habits given by the blacks, and several other items of evidence, however, would point to its being largely phytophagous, or at least less rhizophagous than *Bettongia*, *Potoröus*, and *Aepyprymnus*. In this connection, too, it may be noteworthy that the teeth in all the skulls show a heavier incrustation than in the other genera. It appears to be quite independent of surface waters, since these are quite absent from the greater part of its range, and when they do occur there is no evidence that any use is made of them. Five miles from the area where most of the specimens were secured is a semi-permanent waterhole with the usual gently shelving clay margins; no tracks of *Caloprymnus* were there, however, although the water had been there for many months. It is curious that the animal should shun the sand-hills, since the chief succulent plants of the district, *viz.*, the *Parakeelia* and *Munyeroo*, which might be thought its readiest means of acquiring a water intake, occur very sparsely, if at all, on the flats.

The seasonal aspects of reproduction in *Caloprymnus* would appear to be much the same as those of *Bettongia lesueuri*, as given by Wood Jones (Mammals of S. Austr., pt. ii., p. 212), since of the four adult females obtained in December, three possessed large, furred and partially independent pouch young of a total length of 375, 353, 318 mm., respectively—a very uniform development. The usual irregularities, however, occur, since one adult female in December had a naked pouch embryo of 50 mm., and gave no evidence of having recently suckled larger young. Further, the original specimen obtained by Mr. Reese, in August of the same year, was also an adult female with a pouch young as large as any seen in December, and again in June of this year three females taken by the blacks at Mulka possessed young in widely different stages of growth. Probably the polyoestry proved by Flynn for *B. cuniculus* in Tasmania is common to the whole subfamily. In no case was more than one embryo present in the pouch, but in one female, two of the total four mammae were functioning.

The data at present available are quite insufficient to give reliable information regarding the normal sex ratio of the species, and as already mentioned the methods adopted in obtaining a considerable proportion of the specimens tend to give females rather than males; yet even with these reservations, it is certainly curious that of the eighteen specimens<sup>(7)</sup> examined thirteen should be females.

#### EXTERNAL CHARACTERS.

Although so little has previously been known of the distribution and general economy of the animal, the three original specimens in the hands of Gould, Waterhouse, O. Thomas and Bensley have yielded a sufficiently full account of its characters to establish its systematic position. Having been based, in large part, on filled skins, however, they are misleading in some particulars, and occasion is here taken to correct them and to add further detail which has been obtained by observation and measurement of a series of developmental stages in the flesh.

The series available (Table 1) does not include a fully adult male, but there can be no doubt that the animal is one of the smallest of the *Potoröinae* and is inferior in most of its linear dimensions and in weight to all the species of the subfamily, with the possible exception of the little known *Potoröus gilberti* and *P. platyops*. The absence of an adult male is unfortunate, as it leaves unsettled

<sup>(7)</sup> For opportunities of examining five of these taken since my return from the district, I am indebted to Mr. C. W. Brazenor and the authorities of the National Museum, Melbourne.

the interesting question of the relative size of the sexes. The measurements of the aged male in the British Museum given by Thomas are taken from a filled skin and, except for the pes, are, therefore, of little use for comparison. The foot length given, however (21 mm.), is only 2 mm. in excess of that for a male in the present series at the P<sup>3</sup>M<sup>2</sup> stage, from which it may perhaps be inferred that the maximum dimensions attained are not greatly in excess of those quoted in the Table. If this is so, then the female is probably larger than the male, as I have recently shown to be the case with *Aepyprymnus*, and as occur in many genera of *Phalangeridae*. If the stage of dentition is taken as a criterion of the general development of the animal, *Caloprymnus* appears to exhibit individual variations in size considerably greater than anything I have been able to observe in series of *Bettongia*, *Aepyprymnus*, and *Potoröus* culled from a restricted locality. But it is possible that interruptions in the tooth succession are responsible for some (though not all) of the anomalies which occur.

Thomas states that the form is slender and delicate. Skins may be made to appear so perhaps, but there is little in the appearance of the animal to distinguish it in this regard from the Bettongs. The long tail and neatly-formed pes may merit these terms, but the body is thick and even bloated in older animals and the blunt head and short neck quite destroy any impression of slenderness. In general shape, the animal is reminiscent of *Aepyprymnus*.

The head (pl. viii., fig. 1) presents several strongly-marked characters, which confer upon it a striking physiognomy sufficient to distinguish it at once from all its allies. In a frontal view (pl. viii., fig. 2) its outlines are such as might be inferred from the shape of the skull—the muzzle being very short and conical and tapering rapidly from an unusually broad interorbital region. It is the profile view, however, which is so strange and so characteristic and for which one is quite unprepared by the cranial outline. In this aspect the muzzle is abruptly and vertically truncated, and the upper lips, which are enormously developed, swell outwards beyond the level of the rhinarium, and in so doing add greatly to the curious bluff expression of the face. The nasal profile is strongly concave and rises rapidly to a markedly convex supra-orbital and frontal region—the condition is exaggerated as age advances, but it is always noticeable even in the sparsely furred young. The rhinarium is large, naked, smooth or obscurely tessellated and nearly black in colour. It is broader than deep, its transverse diameter exceeding the vertical by  $\frac{1}{3}$ . At no stage does it show any sign of being cleft in the midline. The facial vibrissae are rather poorly developed, and submentals and interramals are apparently absent. The mysticals are flexed strongly forward; four which occupy the antero-superior corner of the set are black, but the remainder are white. The genals and supraorbitals are entirely black. The eye is prominent and staring, its pupil almost circular and very dark bluish-brown or black in colour. The lids are prominent and fleshy.

The ear is a remarkable feature and differs considerably from that of *Aepyprymnus*, *Bettongia*, and *Potoröus*. In the adult or subadult animal the auricle attains a length from the tragoid notch to the distal margin of 45 mm., and its maximum transverse breadth falls as low as 14 mm. It is thus longer and narrower than in any other animal in the subfamily. Its shape is peculiar in that it is deeply entroughed, the lateral margins are parallel for the greater part of their length, and the external surface of the pinna is indented by a shallow longitudinal sulcus. Its substance is thick and fleshy, and the inner naked portions are in most of the specimens pigmented black as in the *Macropodinae*. The sculpture of the cartilage is simpler than in the other three genera. The helix is well developed basally but has little distal extension as a marked feature. The anti-helix is low and ill-defined and without accessory or associated processes. The tragus is well marked but small, and is separated by a very distinct notch from a



low anti-tragus from which springs a conspicuous tuft of light-coloured hairs. In life, the ear is apparently rather immobile. It is carried prominently, and as its base is not obscured by long fur on the crown of the head as in other Rat Kangaroos, it bears considerable resemblance to *Lagorchestes*. The ear was described by Gould, Waterhouse, and Thomas alike, as being short and rounded—a further example, if such were needed, of the difficulties which attend the description of soft parts from dried skins.

The fore limb is exceedingly small and feeble, the bones of its three segments weighing but 1 gramme, as compared with 12 grammes for the bones of the hind limb, and the combined lengths of the three segments in fore and hind limbs are as 1:3·1. In the manus (text fig. 3, A and B) the digital formula is  $3 > 4 > 2 > 5 > 1$  but closely approximates to  $3 > 4 = 2 > 5 > 1$  and as the attachment of the lateral digits to the metacarpus takes place at the same level on either side, the arrangement is a symmetrical one. The general condition is similar to that of *Bettongia lesueuri* but the manus is relatively smaller, the digits slighter and the ungual phalanx and its nail notably longer. The interdigital, thenar, and hypothenar pads are fused as in *Bettongia* to form a subtriangular cushion occupying the greater part of the palmar surface; the fusion of the basal pads is less complete, however, in *Caloprymnus* and the hypothenar element is indistinctly marked off by a shallow sulcus. The development of the cushion is greater than in *Bettongia* and in a lateral view of the manus it projects very prominently. The naked portions of the palm are pale horn-coloured and indistinctly granular, and the nails are pale horn-coloured and translucent.

The hind limb is long, but very slight in proportion to the bulk of the animal (pl. vii.), and with the gluteal portions little developed. The ratio of the length of head and body to hind limb is 1:1·03, which is about that prevailing in *Aepyprymnus* and *Bettongia*. Its most conspicuous feature is the relatively enormous size of the pes as compared with the femoral and median segments. It is characteristic of the hind limb of the arboreal *Phalangeridae* that the femoral segment is markedly dominant as regards length, and its relation to tibia and pes is expressed by the formula: Femur > Tibia > Pes. In *Phascolarctus*, for example, the ratios are 400:317:283. The evolution of the characteristic elongated pes of all the terrestrial *Macropodidae* appears to have been achieved largely at the expense of the ancestral phalangerine femur, since there is a marked reduction in the contribution of the proximal segment to the total length of the limb in all genera of the family. The segment ratios in the two subfamilies, however, are constantly different. In the *Potoröinae* the prevailing condition is that Pes > Tibia > Femur; this is true even in the short-limbed *Potoröus*,<sup>(5)</sup> and it is significant that in all species the relation of the tibia to the limb as a whole remains much as it is in the *Phalangeridae*. In the *Macropodinae*, on the other hand, a secondary elongation of the tibia results generally in a more specialized condition, expressed by Tibia > Pes > Femur. In the proportional constitution of its hind limb *Caloprymnus* not only exhibits the condition of the other *Potoröinae* but carries it to such an extreme as actually to reverse the numerical ratios of *Phascolarctus*. In a subadult male of the former the ratio, Femur:Tibia:Pes becomes 262:330:401.

The pes (fig. 3, C and D) is narrow, very elegantly formed, and in general appearance is reminiscent of the smaller *Macropodinae* such as *Lagostrophus* and *Lagorchestes*, rather than *Bettongia* and *Aepyprymnus*. Its proportions, however, are as in the other *Potoröinae*, and the ratio, Pes:4th toe, is as 1:·46—a value very constantly shown by all four genera and much higher than that shown by the *Macropodinae*. The fourth toe is strongly specialized in adaptation to the stony condition of much of the country over which it moves; in an inferior view

(5) Occasionally in old males of *P. tridactylus*. Pes = Tibia > Femur.

its first phalanx is very narrow, but at the second there is a sudden expansion owing to the development of a broad resilient pad, on which the crease line is much reduced or quite absent, and which continues without constriction to the base of the nail. The fifth toe is well developed, and the syndactylous toilet digits are about as in *Bettongia*, but are strongly reflexed distally so that their nails point almost directly upwards and not downwards or forwards as is usual. The interdigital pad is large, oblong, and lies slightly oblique to the long axis of the

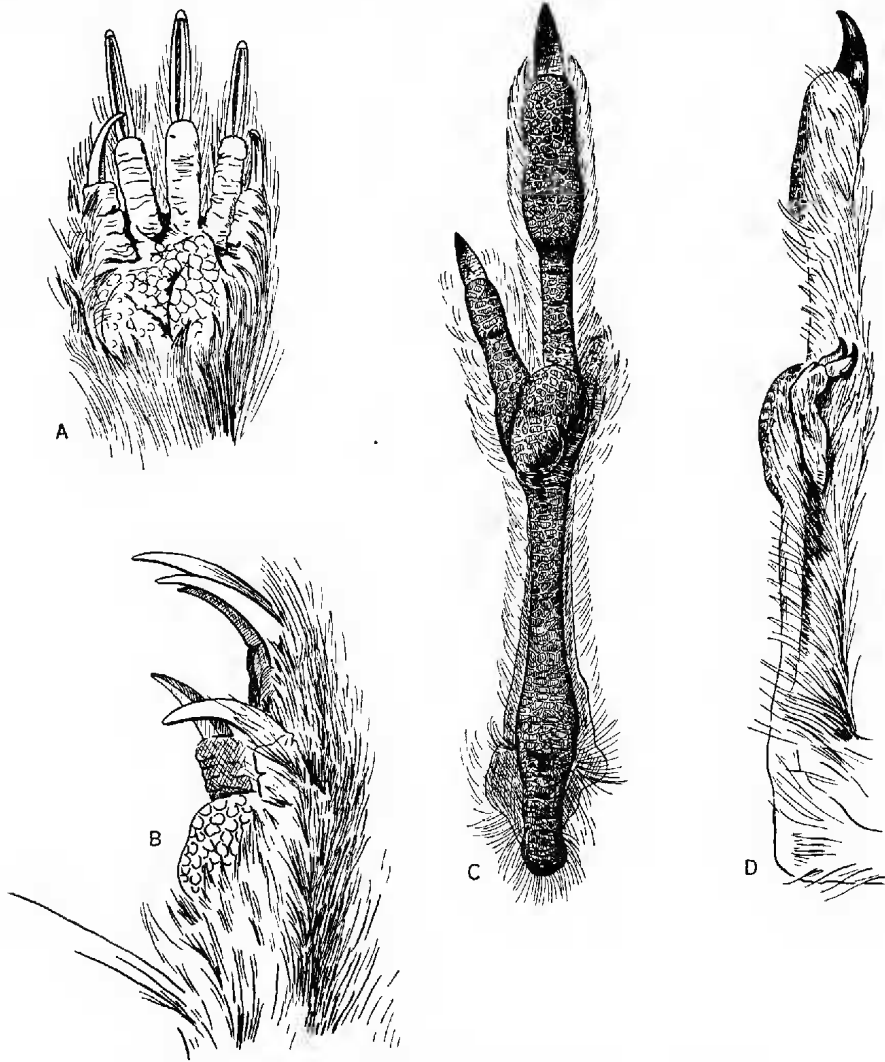


Fig. 3, A, B, C, D.

The manus and pes of *Caloprymnus campestris*; subadult male.  
A and B, Right manus (x2); C and D, Right pes (x1).

foot. The entire extent of the plantar surface of the pes is quite naked and without infringement of hairs upon its margins. The sole is harder and tougher in texture than in *Bettongia*, is rather coarsely granular, and variably pigmented a dark slate or black, but this, like the pigmentation of the auricle, is subject to fading in spirit specimens. The nails are black and opaque. There is a marked and abrupt expansion over the infratarsal sesamoid.

The tail is very long, the ratio of its length to the head and body being 1.16:1, and is thus longer than in any other member of the subfamily. It has little basal thickening, is circular in section and tapers very slowly to the end and is subcylindrical for the greater part of its length. Its distal portion has no modifications suggesting a prehensile function, and it is without either chevron callosities or the basal callous on the upper surface. The post sacral vertebrae in a subadult male number 24.

The cloaca (fig. 4, A and B) in both sexes is small and inconspicuous, with poorly developed margins but little raised above the general ventral surface. It is not surrounded by specialized bristles but from the inferior (caudad) margin, a fleshy club-shaped or subcylindrical process is developed similar to that of *B. lesueuri* but larger and more sharply demarcated. In adults the process is 6 mm. long and pendant, but in four furred pouch young examined it is folded forwards

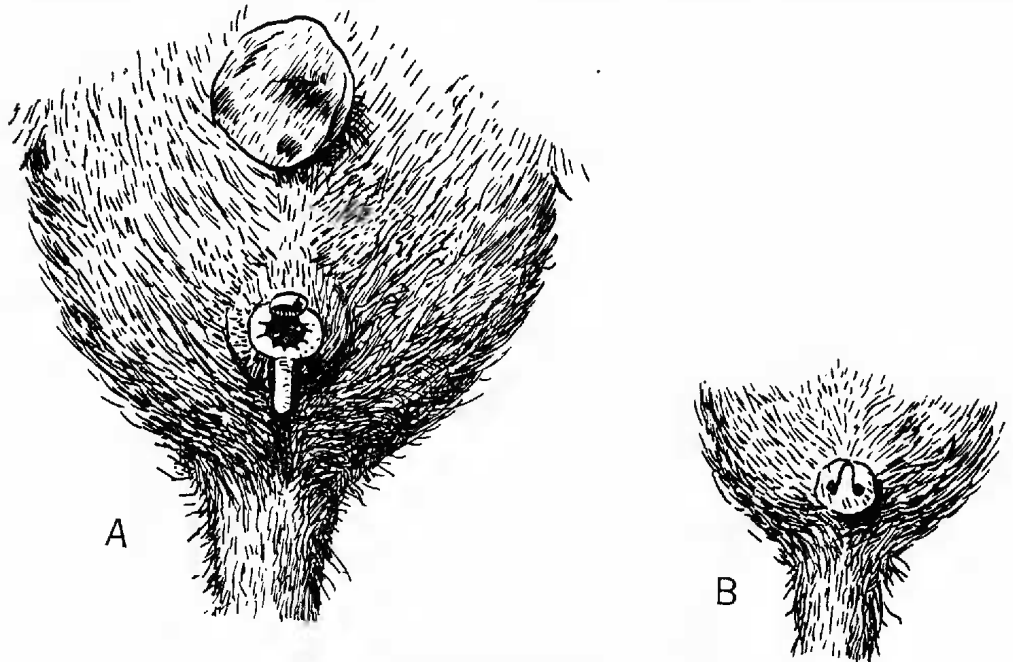


Fig. 4, A and B.

The cloaca of *Caloprymnus campestris*.  
A, Subadult male; B, Female pouch young.

and adpressed so as to cover the orifice. The testes in the four subadult males are rather small, and the skin of the scrotum is unpigmented. In females the opening of the pouch is unusually far forwards, being somewhat anterior to the mid-point of the ventral surface; it has no anterior extension but is produced posteriorly almost to the cloaca. The mammary area is surmounted by four nipples, either one or two of which are functional.

Between the insertion of the fore limbs, sternal or gulo sternal in position is the naked area which has been noted in previous descriptions. It is present in all the specimens obtained, both male and female, and is quite distinct even in the furred-pouch young, though its boundaries become more sharply defined as age advances. There is a good deal of variation, apparently individual rather than sexual, in its shape and exact position, but it is commonly about 50 mm. long and 20 mm. wide, and roughly oblong or lozenge shape; its longitudinal extension is always much greater than its transverse. When incised the skin does appear to

be especially thickened or modified and to the naked eye it presents little evidence of a glandular function, being smooth, poreless and unstained by exudates. It is not surrounded by hairs specialized in colour or texture as in *Trichosurus*, *Petaurus*, and *Phascolarctus*. The peculiar swollen, almost goitred, appearance of the throat in one of the examples figured by Gould, was not presented by any of the present series.

#### PELAGE.

As the descriptions of Waterhouse and O. Thomas on this head may be applied without serious discrepancy to the skins now available, and as Gould's plate is on the whole an excellent representation of the animal, it will be unnecessary to give a detailed systematic description. It may be well, however, to restate the coat colours in terms of modern standards and to refer briefly to those pelage characters which tend to mark it off from its allies.

The longest hairs of the dorsum reach 35 mm. in length, and the coat, which is very soft to the touch, is dense and has a copious under-fur; a curious condition in an animal partially diurnal in habit and exposed throughout a large part of the year to excessively high day temperatures. There appears to be little seasonal variation in the coat. In the mid-dorsal region the fur presents five distinct colour zones. The under-fur (which is of about equal diameter throughout its length) is close to Ridgeway's "blackish slate" for its basal  $\frac{2}{3}$ ths. The median portion of equal length is about "cinnamon buff," and the terminal  $\frac{1}{3}$ th a rich blackish brown. The guard hairs in their basal  $\frac{2}{3}$ ths are "blackish slate," this is then succeeded by a narrow band of rich blackish brown, a broad subterminal band of "ivory yellow," and the extreme tip, which is finely pointed, is rich blackish brown, shading into black. The basal portions of the guard hairs are circular in section and of about the same diameter as the under-fur (.04-.06 mm.), but at the subterminal band there is a rather rapid expansion to a maximum of .31 mm., and this light-coloured portion is quite opaque and is highly modified in shape, taking the form of a flattened blade .13 mm. thick, tapering at both ends and distinctly grooved on one surface. In the mid-dorsal area, the sequence of the very pale subterminal band upon the dark brown zone affords a striking contrast when the fur is parted, but on the nape and sides the brown band tends to disappear, and on the rump the basal slate band, also, is much reduced. The ventral fur is creamy white distally, darkening to a very pale slate basally. In spite of these contrasted colour zones, the dominant impression conveyed by a general view of the animal at a little distance is of its extraordinary pallor, produced by the heavy uniform overlay of guard hairs carrying to the surface of the coat the broad yellowish white subterminal band. The arrangement of these bands is so close and dense on the dorsum that the brown and ochre tones in the deeper layers of the coat are quite obscured, and as their flattened surfaces possess a curious opaque nacreous lustre, a reflecting surface is produced more effective perhaps than in any other marsupial, except *Notoryctes*. O. Thomas gives the general colour as "grizzled sandy," but if the skins are viewed at such a distance that the component colours blend into a uniform whole (and this seems to be the rational procedure in determining a general colour) they approximate to Ridgeway's "light buff." Theories of protective and adaptive colouration have been carried to such lengths that one hesitates to adduce new instances of it, yet the resemblance of the pale buffy tones of the pelage to those which prevail in much of the country where the animal was observed, is too remarkable to be passed over without comment.

As is general throughout the subfamily, there is an entire absence of distinct body or face markings, but the ear which has generally been described as uniformly coloured, is strongly bicolor on its outer surface in all the specimens examined. A narrow area adjoining the anterior margin is clothed with short rather coarse

adpressed hairs of colour near to Ridgeway's "ochraceous tawny," but the remainder is rather sparsely covered with light cream, fluffy hair which fails to conceal the black epidermis; the areas involved and their condition is much as in *Aepyprymnus*, though the contrast is not so marked as in that animal. These pale fluffy hairs lengthen as they approach the base of the ear, where they finally merge with a prominent creamy white patch of similar texture having its origin at the intertragoid notch. In the profile view of the head this is a conspicuous feature; it is not present in any other of the *Potoröinae*, but in a reduced form is a familiar feature in many wallabies.

In the young animal the tail is covered with short adpressed hair, bright yellow above, paler below. The hairs on the upper surface are so sparse as to reveal the epidermis, but below they are plentiful, coarse, translucent and closely adpressed. In older animals most of the hairs of the upper surface are lost and the scales of the almost naked epidermis may then be seen to average 11 rows per centimetre, the under surface of the tail retains its dense covering through life, and its condition is exactly that of the typical wallabies and kangaroos. In one specimen only is the tail-tip white.

The hair tracts are much as in *Aepyprymnus*—cephalo-caudad and proximo-distad dorsally, ventrally a strongly marked central opposition ridge especially in females and a gular reversal. Seasonal, sexual and individual variation in pelage characters are but little evident. The closeness of grizzling and the colour is influenced somewhat by age, younger animals appearing more fulvous and less grizzled, owing partly to an inferior development of guard hairs and partly to a richer tone in the outer subterminal band and in the under-fur.

The furred pouch young is very like the adult in colour, such differences as occur being due chiefly to a scantier development of under-fur and to a light sprinkling of black hairs over the dorsum.

#### SKULL CHARACTERS.

Eleven skulls have been examined (Table 2), representing stages from pouched young with incomplete incisor series to aged individuals with worn  $P^4M^4$ . The skull attains its maximum dimensions at an early dental stage, and in spite of the range of development represented, the series is a uniform one owing to the early setting of the suture lines into forms which are not much modified by increasing age; a peculiarity shown by all the *Potoröinae* and strongly contrasted with the marked time changes which are the rule amongst the *Macropodinae*. With the possible exception of *Potoröus platyops* the adult skull is the smallest of the subfamily, but at the same time is relatively the broadest and in general appearance is very different from all the related forms whose main quantitative inter-relations are summarized in Table 3.

Theoretical interest centres chiefly in the structure of the muzzle region and in the dentition.

The short, excessively broad narial chambers (fig. 5, A) constitute by far the most striking feature of the skull, and serve at once to distinguish it from all other *Macropodidae*. The condition at first sight suggests a highly specific modification for the housing of an enlarged ethmoturbinal. This may be partly so, but when the dimensions of the muzzle region in *Caloprymnus* are compared statistically with the rest of the subfamily the modification is seen to be rather less significant than it at first appears. If consideration be given to the relative size of the skulls of the different forms, it is seen that the brevity of the muzzle is exceeded in the central forms of *B. lesueuri* and its breadth is closely approached by *P. platyops*. The circumstance of the occurrence of a similarly enlarged ethmoturbinal in both *Caloprymnus* and *Potoröus* argues strongly against the adaptive character of this feature, since the two genera occupy the climatic extremes of

the continent, and there can be little doubt that it represents a primitive character carried over from the ancestral *Phalangeridae*. It may be noticed that amongst existing species of the last family, *Petaurus australis*, which according to Bensley

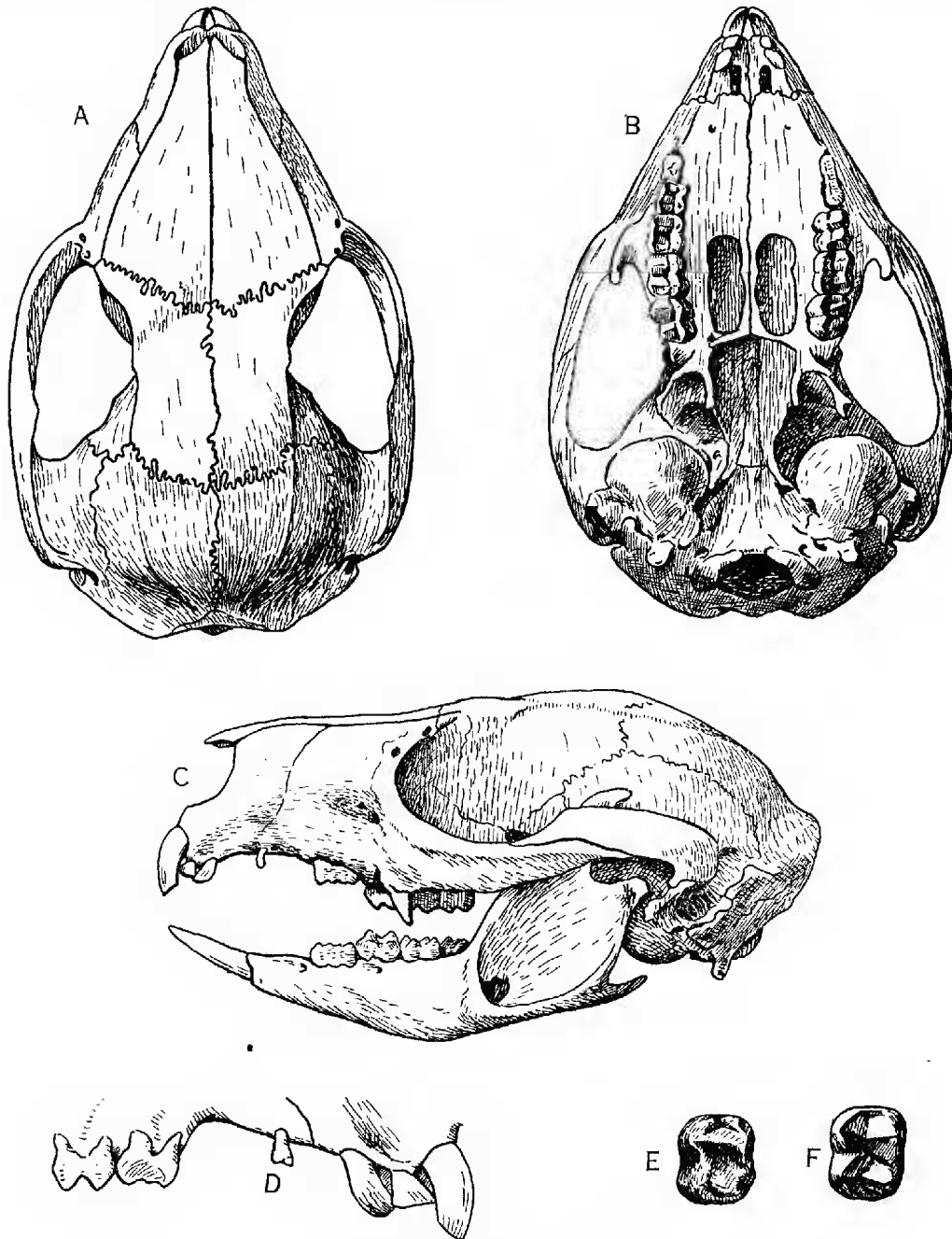


Fig. 5, A, B, C, D, E, F.

A, B, C, Frontal, palatal, and lateral views, respectively, of the skull of *Caloprymnus campestris*, an adult female (x2). D, Side view of anterior palate of an immature male, to show the vestigial diastemal tooth (x2.6). E, Left upper 2nd molar figured by Bensley (after Bensley). F, Left upper 2nd molar of a young male (x2.6).

should not be far removed from the root stock from which the *Potoröinae* sprung, presents features in its muzzle region distinctly recalling those under discussion.

The development of the nasal bones themselves is still more curious and more characteristic of the animal as a structural feature, than the chambers which they cover. They are of enormous size, and are so developed in all directions that the premaxillae, maxillae, lacrymals and frontals which in the other forms make appreciable contributions to the roofing of the nares are in *Caloprymnus* crowded out to the margins of the turbinal areas. Their breadth is immediately apparent on inspection of the skull, but their great length, while equally remarkable, is only brought out by comparative measurement. By expressing the length of the nasals as a percentage of the basal length of the skull it is seen (Table 3) that they are longer in *Caloprymnus* than in any other species except *Potoröus tridactylus*—a notable result in view of the general dissimilarity of cranial form in the two. The lengthening of the nasals is effected by an encroachment on the frontals, as is shown by the fact that the posterior margins of the former reach back as much as 6 mm. beyond a line joining the posterior lacrymal foramina. In all other species the nasals fall short of this line, usually by a considerable interval. The broadening of the nasals is definitely an age character, and the condition figured by Thomas and the still more extreme condition shown in fig. 5 A, in which their posterior border is almost transverse, is not shown by immature individuals; in these younger skulls the posterior margins are sinuous in varying degree.

The skull is further distinguished from all other *Potoröinae* by the uniform presence of an infrazygomatic process of the maxilla; the process is well developed and has an average projection beyond the lowest point of the malar of 4 mm. Although the process occurs in a rudimentary form in the larger phytophagous *Phalangeridae*, its presence as a notable feature in the structure of the zygomata is the exclusive possession of the *Macropodinae*, where it has evidently been developed in response to changes in the masticatory apparatus called forth by the adoption of a bulky herbivorous diet. That its presence in *Caloprymnus* rests on a similar functional basis and is correlated with the modifications of the dentition, is strongly indicated by analogy and by such information on its feeding habits as is available.<sup>(9)</sup>

Other minor points of distinction are to be found in the brain case, which is very small and globular with little tapering towards the interorbital region; in the temporal ridges which are strongly marked and in the anterior palatine foramina, which though variable have an average relative length considerably greater than in other rat kangaroos.

Underlying the many aberrant characters of the skull, striking though some of them are, there is, nevertheless, no lack of evidence to associate it in an unequivocal way with the *Potoröinae*. Apart from the testimony of the dentition, one of the most interesting links of relationship is afforded by the condition of the temporal region of the skull, where in *Caloprymnus* the squamosal makes a wide contact with the frontal, as it constantly does in every member of the subfamily. Throughout the Marsupialia the alternative condition of a contact between parietal and alisphenoid is the usual one, and the *Peramelidae* and *Potoröinae* appear to be the only constant exceptions. The feature effects a sharp cleavage between the *Macropodinae* and *Potoröinae*, as throughout the whole of the nine genera of the former I can find no exception to the alisphenoid-parietal contact, which is generally characteristic also of the ancestral *Phalangeridae*.

The mandible is very much as in *Bettongia* and has a long slender coronoid, receding obliquely from the body of the ramus, as in all the subfamily. The condyle is not elongated transversely as in *P. tridactylus*, and the lower border of the body is not more convex than in other species.

<sup>(9)</sup> It must be admitted as an apparent anomaly, however, that *Aepyprymnus*, in which similar modifications of the molars occur, does not develop the process.

## DENTITION.

The dentition as shown by the British Museum specimens has been described and partly figured by O. Thomas and Bensley, and the phylogenetic significance of its characters has been assessed by the latter. Examination of the present series permits of slight modifications and additions to these accounts. P<sup>4</sup> takes its place shortly after M<sup>3</sup>, and judged by the dimensions of the skull and the animal at the time M<sup>1</sup> is late in erupting, not early, as stated by Thomas in his diagnosis of the subfamily. Although no irregularities in the succession of P<sup>4</sup> with respect to the other teeth are presented, the entire development of the posterior arch may be delayed (as in *P. tridactylus*) so that animals which are old when judged by their general size, and their sutural and epiphysial conditions, come to have a juvenile dentition. Thus the skull of the largest examples obtained (fig. 5, B), in which the age characters of the nasals and temporal crests are more marked than in any others, is just at the tooth change and still lacks an M<sup>4</sup>.

In the incisor series, canine and premolars, all the modifications listed by Bensley as being prototypal to the *Macropodinae* are to be seen. It may be noted, however, that the tooth which has been called a canine is usually erupted somewhat posterior to the premaxillary suture, and although its vestigial nature is attested by its great variability, yet in young skulls it is far from caniniform, since it widens distally to form a distinct cuspidate crown (fig. 6) and then resembles somewhat the bifid premolars of the simpler *Phalangerinae*. P<sup>4</sup>, in its unworn condition, has in addition to the postero internal talon a distinct *antero internal* ledge which runs back nearly half the length of the tooth.

It was stated by Bensley that the upper molar teeth decrease gently in size backwards, but in the present series the condition is less primitive since in both upper and lower jaws 1<2>3>4 as it usually is in *B. lesueuri*. The upper M<sup>4</sup> is a very small tooth in the two examples, in which it is fully erupted but unworn; it is tricuspid and triradical and the posterior lobe shows no bifurcation. The lower M<sup>1</sup> is larger but otherwise similar in character. Hypsodontism is shown by the outer cusps of the upper molars much more than by the inner cusps, and *vice versa* in the lower series, and the difference in height is rapidly accentuated by wear, so that as age advances the occlusal plane rapidly becomes oblique to that of the palate, as it does in the hypsodont section of the *Macropodinae* and to a lesser degree in *Aepyprymnus*.

The modifications of crown pattern away from *Bettongia* and towards the *Macropodinae*, although recognisable, are somewhat less evident than might be gathered from Bensley's description and figures. The tendency for the transverse ridges of the outer cusps of the upper molars and the inner cusps of the lower molars "to extend to the remaining cusps" is not greater than in unworn molars of *B. lesueuri* for example, and much less than in *Aepyprymnus*, and no unworn molar in the present series shows so extensive a development of the anterior transverse crest as in his pl. 5, fig. 19.<sup>(10)</sup> (Compare fig. 6, E and F.)

In all the specimens now examined the buccal cusps of the upper molars, and the lingual cusps of the lower series, make a much greater contribution to the transverse crests than their fellows on the opposite side. On the other hand, the longitudinal elements of the upper lingual cusps are strongly marked, and in particular that which proceeds from the posterior of them obliquely forwards towards the central valley of the crown is more prominent than in all the genera except *Aepyprymnus* and occupies about the same position as the "central connecting bridge" in *Macropus*. The resemblance of the newly erupted crowns to those of *Trichosurus* is striking.

<sup>(10)</sup> This may be partly due to the difficulty of representing vertical elements in a full crown view.



Although in no way affecting the claims of *Caloprymnus* to a prototypal position with respect to the dentition of the *Macropodinae*, it is of interest to note that *Aepyprymnus* in the perfecting of the transverse ridges, in the development of longitudinal elements, and in increased hypsodontism, has independently attained to a much more advanced position.<sup>(11)</sup>

In the relative length of its molar series, *Caloprymnus* exceeds all other *Potoröinae*.

#### SKELETON.

Comparisons instituted between the skeleton of a young male *Caloprymnus* and other members of the subfamily have not disclosed differences of importance. While individual variation is considerable, generic and specific differences in structure are slight and can be brought out adequately only by statistical treatment on series of skeletons at comparable stages, and these are not yet available.

#### RELATIONSHIPS.

Chiefly from an examination of the dentition, Bensley has shown that the subfamily *Potoröinae* of the catalogue of 1888, together with *Hypsiprymnodon*, comprises two groups of genera which are not only marked off from one another by characters which persist through considerable series of forms, but which actually represent diverse or even opposed lines of evolution. *Hypsiprymnodon*, *Bettongia*, and *Aepyprymnus* (6 stages) are characterised by the possession and increasing development of elaborate vertically fluted sectorial premolars, which show a progressive rotation of their long axis through 90° in response to a progressive shortening of the muzzle region, and *Potoröus* and *Caloprymnus* in which the premolar is not fluted, has its long axis in line with the molar series and in which the trend through the three serial forms has been towards a progressive elongation of the muzzle.<sup>(12)</sup> Although both series retain many primitive *Phalangerine* characters and are sharply severed from the dominant subfamily, the *Macropodinae*, yet the second of them is distinctly more primitive than the first.

The special interest of *Caloprymnus* is twofold. On the one hand, it has taken no part in the elongation of the muzzle which is the particular evolution of *Potoröus*, and has acquired by adaptation to a new environment a series of specializations which while rendering it remarkably divergent from its best known living ally, *Potoröus tridactylus*, have brought it convergently, remarkably near the lower members of *Macropodinae*. On the other hand, of all the existing forms of both series it is the only one which tends even slightly to break down the isolation of the two subfamilies from one another, since alone of all the species it exhibits characters in its incisors, "canine," premolars and molars alike, prototypal to the *Macropodinae*.

The data which have now been gained by the recurrence of the animal and which are herein summarized, while confirming the presence of these prototypal characters, tend strongly also to emphasize its primitiveness, its essential identification with the rest of the *Potoröinae* and the fundamental nature of the cleavage of the two subfamilies, in features other than the dentition. In the latter connection, attention may again be drawn to the constant difference in the structure of the temporal region and in the segmental ratios of the hind limb. It is remarkable

<sup>(11)</sup> This comparison is based on Queensland examples of *Aepyprymnus* only, while Bensley's examination was probably confined to N.S.W. examples. It is possible that regional differentiation may have produced considerable changes in the dentition, as it has in *B. lesueuri* and *P. tridactylus*.

<sup>(12)</sup> Bensley created a new group or subfamily for the first series which he called the *Bettongiinae*, and restricted the old term *Potoröinae* to *Potoröus* and *Caloprymnus*. This arrangement, however, as Bensley admitted, was founded on a rather narrow base of characters and has not been widely used. In this paper the term *Potoröinae* is used in the older sense.

that the specialization of *Caloprymnus*, which in the living animal most strongly recalls the higher *Macropodinae*, namely, the perfection of its saltatory habit and performance, should have produced no modification in the primitive proportions of the hind limb, and the circumstance may argue the comparatively recent nature of this development.

The distribution of the animal as now ascertained, isolated as it is from that of the rest of the subfamily,<sup>(13)</sup> and restricted to a comparatively small area of strongly-marked physiographical and climatic features, is sufficient to account for its peculiar specific characters and is of the greatest value as affording a possible clue to the origin of the aberrant evolution which has sundered it so far from the existing species of *Potoröus*. The palaeontological testimony to the past distribution of Australian mammals is so incomplete that it is impossible to form a clear idea of the regional limitations of the various radiations or of the times and routes by which some of the families and genera have acquired transcontinental representation. The geological history of the Lake Eyre Basin, however, seems to be sufficiently known, and its past efficacy as an "active distributing centre" (in W. J. Gregory's phrase) sufficiently well attested, to justify the view that the evolution of *Caloprymnus* from the ancestral *Potoröus* postulated by Bensley, may have begun here.

During a lacustrine phase of relative humidity and bush vegetation, conditions well suited to the sedentary, local, sheltered life of *Potoröus* would be presented, and the subsequent desiccation which proved so disastrous to the already over-specialized *Diprotodon* might awake a successful response in a primitive and plastic form at the level of *Potoröus platyops*, culminating in the relatively perfect adaptations of *Caloprymnus* to the present extreme eremian conditions.

Where *Diprotodon* failed, *Caloprymnus* may yet succeed, but all the evidence of its physical structure is not more eloquent of changed conditions than its pathetic clinging to its flimsy grass nest, in a fiery land where a fossorial habit has become the main factor in survival.

TABLE I.  
Flesh Dimensions of *Caloprymnus campestris* in mm.

♂

	Teeth	Head and Body	Tail	Chest	Manus.	Nail of 3rd Digit*	Pes.	4th Toe.	Nail of 4th Toe.	Ear.	Rhinarium to Eye.	Eye to Ear.	Eye: Canthus to Canthus.	Weight in Grammes (approx.)
1234	P <sup>3</sup> M <sup>2</sup>	272	333	125	21	10	119	55	14	45 x 19	26	21	—	850
1244	P <sup>3</sup> M <sup>2</sup>	282	317	—	22	11	117	56	14	42 x 15	29	21	12	850
1239	P <sup>3</sup> M <sup>2</sup>	263	307	130	21	11	112	51	13	44 x 15	27	22	—	850
1233	—	255	297	130	20	11	106	49	9 (worn)	42 x 13	26	18	—	637
1236	P <sup>3</sup> M <sup>1</sup> P <sup>4</sup>	163	155	—	—	—	84	—	—	26 x 14	19	16	—	140
							♀							
1399	P <sup>1</sup> M <sup>3</sup>	—	377	—	—	—	115	—	—	—	—	—	—	—
1235	P <sup>3</sup> M <sup>3</sup>	275	340	150	20	10	106	49	13	41 x 15	28	23	13	1060
1237	P <sup>4</sup> M <sup>4</sup>	277	328	140	21	11	112	50	14	42 x 15	31	25	11	1060
1216	P <sup>1</sup> M <sup>3</sup>	254	320	150	18	11	104	48	13	42 x 15	28	24	12	1060
1242	—	263	310	125	20	11	108	49	13	41 x 16	26	22	13	743
1217	P <sup>3</sup> M <sup>1</sup> P <sup>4</sup>	163	212	—	—	—	98	—	—	31 x 15	20	13	—	195
1238	—	—	180	—	14	6	96	42	10	30 x 14	21	16	—	135

(13) *B. lesueuri* occurs to the west and north-west of Lake Eyre, but no other species of the subfamily shares the proved habitat of *Caloprymnus*.

TABLE II.  
Skull Dimensions of *Caloprymnus campestris*.

	♀					♂				
	1216	1217	1235	1237	1339	1234	1236	1239	1244	
Number of specimen	1216	1217	1235	1237	1339	1234	1236	1239	1244	
Dental condition	P <sup>4</sup> M <sup>3</sup>	P <sup>3</sup> M <sup>1</sup>	P <sup>4</sup> M <sup>3</sup> (m <sup>4</sup> )	P <sup>4</sup> M <sup>4</sup>	P <sup>4</sup> M <sup>3</sup>	P <sup>3</sup> M <sup>2</sup>	P <sup>3</sup> M <sup>1</sup> P <sup>4</sup> (m <sup>1</sup> )	P <sup>3</sup> M <sup>2</sup>	P <sup>3</sup> M <sup>2</sup>	
Greatest length	60.0	44.0	61.0	61.5	63.5	57.5	38 ca.	60.0	59.0	
Basal length	52.0	35.0	52.0	52.5	54.0	49.0	—	50.5	51.0	
Zygomatic breadth	39.0	27.5	38.0	40.0	40.5	36.0	—	35.5	36.0	
Nasals length	26.5	16.5	28.0	27.0	29.5	24.0	16.0	26.5	27.5	
Nasals greatest breadth	18.5	12.5	18.0	19.0	21.5	19.5	11.0	17.0	17.0	
Nasals least breadth	6.5	5.0	7.0	9.0	7.0	7.5	5.5	7.5	7.0	
Nasals overhang	5.5	2.5	4.5	5.5	4.5	3.5	—	4.5	4.0	
Depth anterior nares	13.0	10.0	13.0	13.0	13.5	12.5	—	13.0	12.5	
Constriction	14.5	11.5	14.5	14.0	15.0	14.5	—	13.5	12.5	
Palate length	33.0	22.0	32.0	33.0	33.5	30.5	—	31.0	32.0	
Palate breadth inside M <sup>2</sup>	12.0	—	11.5	12.5	12.0	10.5	—	11.0	10.5	
Ant. palatine foramina	5.5	3.0 ca.	3.5	6.0	3.5	2.5 ca.	—	3.5	3.0	
Diastema	8.5	5.5	8.0	9.5	10.0	7.5	—	8.5	8.5	
Basicranial axis	18.0	12.0 ca.	19.5	18.5	19.0	17.0	—	18.0	18.0	
Basifacial axis	35.5	25.0	35.0	35.0	36.5	33.0	—	34.5	34.0	
Facial index	197	208	179	188	192	194	—	191	189	
M <sup>s1,3</sup>	13.0	—	12.5	11.5	12.5	8.5	—	8.5	8.0	
						(M <sup>s1,2</sup> )		(M <sup>s1,2</sup> )	(M <sup>s1,2</sup> )	
P <sup>3</sup>	—	3.5 ca.	—	—	—	3.5	3.0	3.5	3.0	
P <sup>4</sup>	6.0	—	5.5	5.5	5 ca.	—	—	—	—	

TABLE III.

Skull Dimensions of *Potoröinae*, expressed as percentages of the basal length and derived from mean values of series of both ♀ and ♂ at the P<sup>4</sup>M<sup>4</sup> stage.

	<i>Aepyrymnus rufescens</i> .	<i>Bettongia lesueurii</i> .	<i>Bettongia cuniculata</i> .	<i>Bettongia (†) gainardi</i> .	<i>Bettongia penicillata</i> .	<i>Potorous tridactylus</i> .	<i>Potorous (†) gilberti</i> .	<i>Potorous (†) platyrops</i> .	<i>Caloprymnus campestris</i> .
Basal length	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
Zygomatic breadth	69.3	71.2	65.3	68.5	61.5	60.1	55.8	70.0	74.9
Nasals length	38.0	47.0	48.6	47.2	47.1	55.2	51.4	48.0	50.7
Nasals greatest breadth	23.1	21.2	20.8	24.5	18.8	17.4	19.8	26.0	36.5
Nasals least breadth	13.6	9.8	10.7	14.1	9.4	7.7	8.8	9.2	14.1
Nasals overhang	11.5	10.6	10.4	—	9.4	9.9	—	—	9.5
Depth anterior nares	22.4	21.2	20.5	—	21.7	19.1	—	—	24.8
Constriction	22.4	21.2	27.8	29.4	26.0	24.8	25.0	29.2	29.4
Palate length	65.3	63.6	65.3	69.2	66.6	69.7	64.7	60.0	62.7
Palate breadth inside M <sup>2</sup>	24.4	21.2	21.2	22.3	20.2	19.8	19.1	20.0	22.8
Ant. palatine foramina	4.1	6.0	6.2	4.7	5.8	5.3	5.0	4.2	9.1
Diastema	13.6	13.6	19.0	18.8	19.5	20.2	20.6	15.6	17.0
Facial index <sup>(2)</sup>	214	181	234	225	213	264	—	—	189
M <sup>s1,3</sup> $\left. \begin{matrix} M \\ A \\ X \\ I \\ A \end{matrix} \right\}$	21.7	20.4	19.5	20.1	18.1	19.7	17.6	17.8	23.4
P <sup>3</sup>	9.5	6.8	7.8	—	5.8	6.9	—	—	6.6
P <sup>4</sup>	12.1	12.8	12.0	10.2	10.1	9.5	8.1	9.8	11.4

(1) One example only: From B.M. Catalogue of Marsup. and Monotrem, 1888.

(2) Unmodified.

## ACKNOWLEDGMENTS.

In addition to the constant help rendered by Mr. Reese, I have to acknowledge many courtesies from other residents in the area traversed. In particular, I would extend my thanks to Mounted Constable John Finn, of Innamincka, whose knowledge of the eastern fringes of the gibber country has been of great value.

For assistance in various matters in connection with the preparation of the paper, I am further indebted to Mr. H. Condon, of the Museum staff, to Miss Huldah Fornachon, and to Mr. Colin Kerr Grant.

## EXPLANATION OF PLATES.

## PLATE VII.

*Caloprymnus campestris*. General outline of subadult ♂, from a photograph taken a few seconds after death.

## PLATE VIII.

Fig. 1. *Caloprymnus campestris*. Profile view of the head of an adult ♀.

Fig. 2. Front view of adult ♀.

## PLATE IX.

Types of country in the habitat of *Caloprymnus*.

Fig. 1. The gibber plains. A view of Sturt's Stony Desert, showing glare on the gibbers in the early morning sun.

Fig. 2. A sandridge—claypan unit, near Clifton Hills Station.

## CORRIGENDUM.

Vol. iv. (1931), p. 75, line 30, from top:—*For*, "and in no part of the valley was I able to examine whether their habitats overlap," *Substitute*, "and in no part of the valley I was able to examine do their habitats overlap."